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This volume is dedicated to Dr. Rainer Zangerl

## New Information on the Evolution of the Bradyodont Chondrichthyes

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### INTRODUCTION

Among the taxa of Chondrichthyans from the upper Mississippian Bear Gulch Limestone of Montana (Lund, 1974; Lund and Zangerl, 1974) are holomorphs of four petalodonts, two cochliodonts, and a chimaeroid. These forms have all been included by various authors within the Holocephali, or Bradyodonti, usually ranked as a subclass within the Chondrichthyes (Arambourg and Bertin, 1958; Obruchev, 1967). Holomorphs of bradyodont fish are extremely rare (Patterson, 1965) and considerable controversy surrounds the inter-relationships of the Bradyodonti and the phyletic position of the group (Patterson, 1968; Bendix-Almgreen, 1968; 1970). This paper attempts to relate some new information to the evolution of the Bradyodont chondrichthyes.

**CLASS CHONDRICHTHYES:** The Chondrichthyes are characterized by a cartilaginous endoskeleton which may be superficially calcified; an exoskeleton composed of cyclomorial, synchro-morial, or lepidomorial scales which may be lost, modified as cephalic spines, or fused into plates; gill chambers covered by an opercular fold or opening separately to the outside; the absence of an air bladder or lung; otoconia, not compact otoliths in the inner ear which remains open to the outside through endolymphatic ducts. Internal fertilization with copulation is present, males have claspers developed as extensions of the axis of pelvic fins. Eggs, in oviparous forms, are in a horny case and fins are supported by cartilaginous radials, ceratotrichia, or both. Dorsal fins may have an

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anterior spine and be supported by a basal plate or serial basidorsals and radials; paired fins lack spines and are supported by various basal elements.

Stensiö (1963), followed by Patterson (1965) and Miles (Moy-Thomas and Miles, 1971), has claimed relationships between Chondrichthyes and Arthrodires, formalizing this hypothesis with adoption of a "supergroup" Elasmobranchiamorphi (Patterson, 1965, p. 106). Zangerl and Case (1973) and Lund (1974) dispute any close association of Arthrodira and Chondrichthyes, on the basis of no significant apomorphic characters being held in common between the two groups (Denison, 1975).

It is beyond the scope of this paper to analyze holocephalian (Bradyodont) characters in relation to those of the Arthrodira. The weight of evidence of even this summary analysis supports the hypothesis that the Elasmobranchii and Bradyodonti are sister groups of Chondrichthyes; Arthrodires are distantly derived gnathostomes.

### BRADYODONTI

The class Chondrichthyes has been divided into two sub-classes, the Bradyodonti (Woodward, 1921), or Holocephali, and Elasmobranchii. Bradyodonty describes a condition of slowness of tooth replacement, in contrast to the limited retention and rapid replacement of teeth in elasmobranchs. Although Nielsen (1932) notes the many successional teeth of edestids in objection to the bradyodont characterization it must be pointed out that edestids do not seem to shed or replace teeth rapidly, but to accumulate them into dental batteries. Holocephaly describes the fusion of palatoquadrate and neurocranium, particularly as seen in the Chimaeriformes. Recent finds of edestids (Zangerl, 1966), iniopterygians (Zangerl and Case, 1973; pers. comm), and petalodonts (this paper) with a free palatoquadrate demonstrate that the holocephalian character complex has arisen independently several times within the group. The term is inappropriate for the subclass, and should be restricted to members of the typical superorder within the subclass Bradyodonti (Arambourg and Bertin, 1958).

Several other characters are associated with the sub-class Bradyodonti. Principal among these is the operculate condition as contrasted with elasmobranchiate gill chambers. There are no known exceptions and the character contrast is valid at present. It is not

known which condition is plesiomorphous, but both conditions can be found among the *Acanthodii* (Moy-Thomas and Miles, 1971).

Tooth histology as a class criterion is discussed by Radinsky (1961) and Patterson (1965), who claims that a superficial layer of pallial dentine is present only in non-bradyodonts. Patterson (1965, p. 108) mentions pallial dentine in edestids such as *Helicoprion*, however, tooth histology seems like a character of dubious value on the sub-class level (Radinsky, 1961; Bendix-Almgreen, 1968). Branchial arches (Patterson, 1965, p. 109) may lay below the neurocranium where the palatoquadrate is shortened to a preorbital position, a presumably derived and specialized adaptation common to Chimaeriformes, ptyctodont arthrodires, and a number of living teleost fish of perciform persuasion (Gregory, 1933), all of which are nippers and nibblers. In Bradyodonti without fore-shortened jaws, e.g., edestoids (Zangerl, 1966), petalodonts, iniopterygians, and cochliodonts (Bear Gulch), the branchial arches do not lay under the braincase completely. The character is not valid on a sub-class level.

Patterson (1965, p. 109) mentions several other characters of the group (his class Holocephali). They are: hyoid arch complete and unmodified, endoskeleton of cartilage, normally calcified in prisms and exoskeleton of dentine or dentine-like tissue without cellular bone. Specialized scales in rings or half-rings surrounding the lateral line canals is also a frequently mentioned character. The first character is quite controversial (Patterson, 1965, pp. 186-187). The remaining two are plesiomorphous for the class Chondrichthyes and are therefore not valid bradyodont characters. Lateral line ring scales occur in some Bear Gulch elasmobranchs.

The Bradyodonti thus can be presently differentiated from its sister group the Elasmobranchii on two bases, slowness of tooth replacement, and on operculate gill chambers.

The Bradyodonti have been subdivided into 10 generally accepted taxa most recently regarded as orders. These orders are:

- Chondrenchelyes (Chondrenchelyiformes)
- Cochliodontiformes
- Petalodontiformes (Petalodontiformes+/or Janassiformes)
- Psammodontiformes
- Copodontiformes
- Menaspiformes
- Edestiformes (Orodontiformes and Edestiformes)
- Chimaeriformes

Iniopterygii  
Helodontiformes

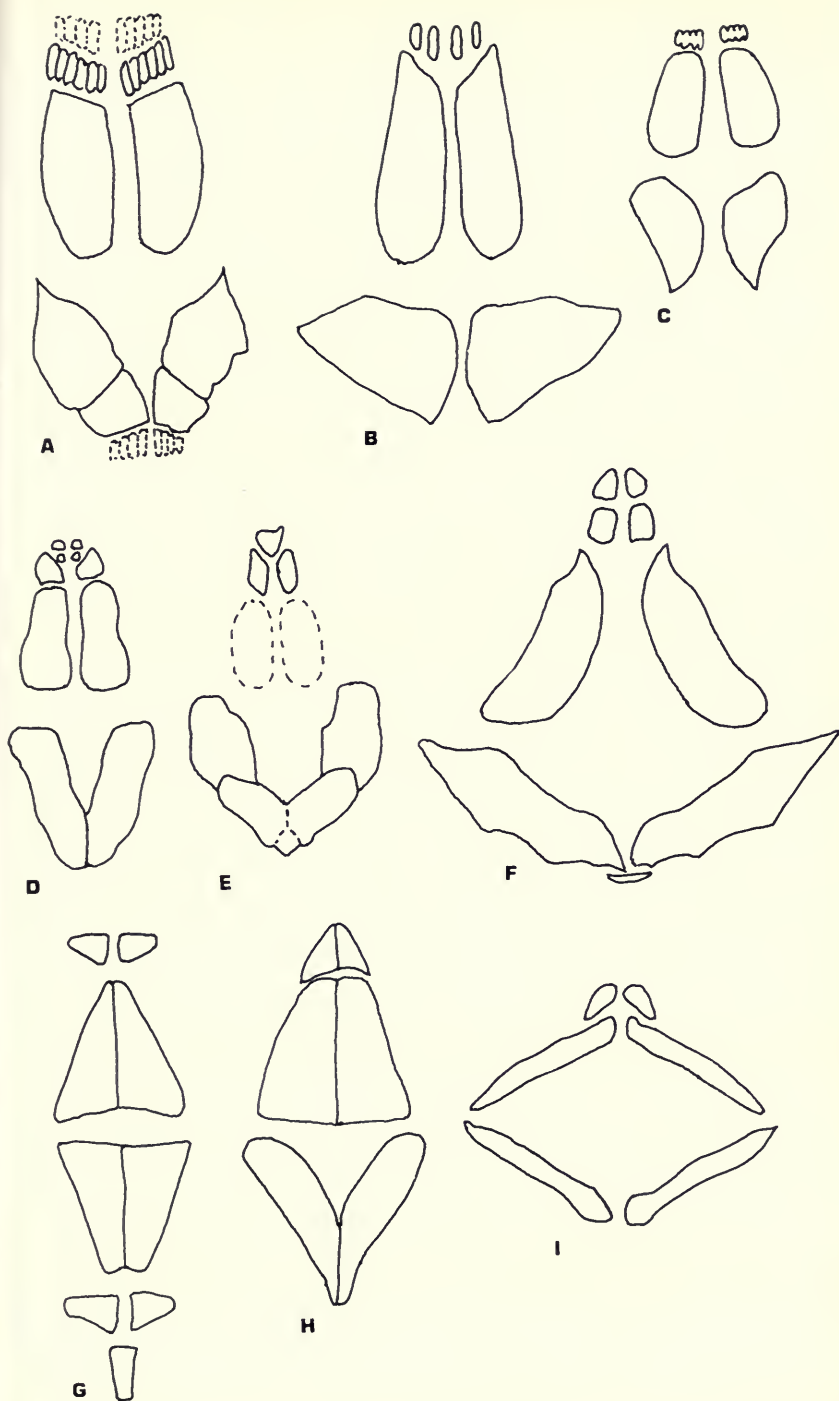
Different authors have grouped these taxa in quite different fashions. Berg (1958) and Obruchev (1967) isolate the Chondrenchelyiformes in a completely separate suprataxon and group the remainder together. Arambourg and Bertin (1958) divide the Bradyodonti into Eubradyodonti and Holocephali, the Holocephali containing chimaeriform-related, Mesozoic and younger families, the Eubradyodonti including the remainder of the equally ranked Paleozoic families. Patterson (1968) divides the Bradyodonti (his class Holocephali) into three orders, Chimaeriformes, Edestiformes, and Chondrenchelyiformes. Bendix-Almgreen (1968) divides the bradyodonts into Chimaeriformes, menaspids and cochliodonts, edestids, helodonts, and chondrenchelyids. Various troublesome forms such as the edestoids *Agassizodus* (St. John and Worthen, 1875) and *Ornithoprion* (Zangerl, 1966), and the petalodonts, as well as psammodonts and copodonts, are placed in incertae sedis (Bendix-Almgreen, 1968, 1970).

Bendix-Almgreen (1970) reinterprets the much-interpreted morphology of *Menaspis* as an arthrodire derivative, with dubious success. His placement of the orbit and orientation of the mouth do not seem implausible. He further develops a thesis of two basic bradyodont dentitional types, a "selachian" type, and a dental plate type. The selachian type contains forms with distinct marginal teeth in a series of tooth families, which span the symphyisial region of the palatoquadrate. The dental plate type shows a limited number of dental plates on each jaw, at the most one or two anterior tooth families, and the dentition divided into separate left and right palatal elements. Bendix-Almgreen ascribes this to the possible fusion in the dorsal midline of the theoretical infrapharyngo-premandibular elements with the palatoquadrates in the selachian type, as opposed to their fusion to the sides of the ethmoid in the dental plate type (Bendix-Almgreen, 1968). The dental plate dentition can be seen to include the Chimaeriformes, Myriacanthi-

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*Opposite:*

FIG. 1. Holocephalian dentitions, diagrammatic anterior view with mouth wide open. A, *Cochliodus contortus*; B, *Deltotoptychius armigerus*; C, *Menaspis armata*; D, *physonemoid*; E, *Synthetodus trisulcatus*; F, *Myriacanthus paradoxus*; G, *Platyxystrodus*; H, *Edaphodon* sp.; I, *Squaloraja polyspondyla*. A, B, after Patterson, 1968; F, I, after Patterson, 1965; C, after Bendix-Almgreen, 1970; H, after Obruchev, 1967; D, G, original; E, after Amer. Mus. Nat. Hist. 7558, 7560.



formes, Cochliodontiformes, and Menaspiformes (fig. 1). *Pleuroplax*, with fewer than eight transverse plates composed of fused tooth families, conforms to the dental plate plan, while *Helodus*, in which only about two of the eight or nine tooth families per ramus are fused into "pleuroplax" plates, does not conform to a dental plate plan (Moy-Thomas, 1936a). The selachian type shows great experimentation, ranging from the simple unicuspid tooth-family whorls of the Iniopterygians (Zangerl and Case, 1973), through various petalodont designs (Lund, in press) to the Edestiform plan. Included groups are the Iniopterygii, Helodontiformes, Chondrenchelyiformes, Petalodontiformes, and Edestiformes.

Taxa which bear a dental plate dentition plan correspond to, and may accurately be called, the superorder Holocephali, for holocephaly is plesiomorphous for the group and is one of several other synapomorphous characters distinguishing it from the second group. The selachian plan group might best be called the PARASELACHII.

*Superorder Holocephali:* Holocephalians are one of the more discrete taxa of Chondrichthyans, and it is useful to consider the pathways of evolution within this group, not only for their intrinsic value but for the insights they afford into the radiations of sister taxa of Bradyodonti. The Holocephali are characterized as follows: holostylic chondrichthyans in which the dentition consists of few large marginal permanent tooth plates, paired tooth families if present, restricted to the anterior portion of the jaws and of the *Helodus* form. There is a tendency to fuse denticles to form dermal cranial armor. The notochord is persistent although dorsal and ventral hemicentra or ring centra may be present and the caudal fin is diphyccercal. The unpaired fins do not form a continuous fold.

The Holocephali are known from several isolated dentitions and many tooth plates and have few Paleozoic holomorphs, several of which are undescribed Bear Gulch upper Mississippian fish. These forms indicated that dentition continues to provide a stable basis for classification and analysis; morphology of the remainder of the fish, where known, does not contradict conclusions drawn from dentitions.

*Cochliodus contortus* mandibular dentition consists of an anterior tooth family and two posterior tooth plates per ramus, while the inferred palatal dentition consists of two anterior tooth families and one elongate posterior plate per jaw (Davis, 1883; Woodward, 1891;

Patterson, 1968). *Psephodus* dentition contained at least three transverse plates per ramus (Davis, 1883; Moy-Thomas, 1963a), as did *Poecilodus jonesi* (Davis, 1883). Davis (1883) illustrates *Deltodus sublaevis* with evidence for three tooth positions, the posterior two of which are plates. Woodward (1891) asserts that there are three plates per ramus in *Pleuroplax*.

The dentition of *Deltoptychius* (Patterson, 1965, 1968; Bendix-Almgreen, 1979) consists of one paired upper family of roughly *Helodus*-like teeth anteriorly and a large posteromesially growing pair of posterior upper plates, and a pair of triangular posteriorly growing lower jaw plates. *Menaspis* reputedly shows fusion of the anterior family into a small anterior ("palatine") pair of plates (fig. 1; Bendix-Almgreen, 1970), a character state derived in comparison to *Deltoptychius*, *Cochliodus contortus* (Patterson, 1968), *C. nobilis* (Newberry and Worthen, 1866), and a Bear-Gulch fish allied to *Physonemus sensu stricto*.

The *Physonemus*-like form is as yet known by only one incomplete specimen. The posterior and lower dental plates conform to *Cochliodus* in general shape, the head is covered by a paired, denticulated shield, there are mandibular spines, the body is covered by placoid (synchronomorial) scales, modified in the dorsal midline into a row of *Listracanthus*-like scales, and the anteriorly placed dorsal fin has a *Physonemus*-like spine followed by a basal plate upon which there are short radials, as in *Ischyodus* (Obruchev, 1967, p. 384). The dentition, squamation, and tendency to cranial plates are compatible with the menaspoid pattern, but this fish lacks the peculiar specializations of the latter group associated with a batoid habitus such as body flattening, loss of the dorsal fin, and development of defensive spines which render *Menaspis* a uniquely derived form.

It is worth mentioning in passing that neither the *Physonemus*-like form nor *Deltoptychius* are the same as *Listracanthus* (Newberry and Worthen, 1870; not Patterson 1965). *Listracanthus* is known from several patches of skin which show the typical scales covering the presumed dorsal surface, and not solely found in one or two specialized middorsal rows.

Among the Bear Gulch chondrichthyans relevant to the present discussion are two other forms, both known by several specimens. The first, close to *Platyxystrodon*, has a dentition which consists of small, deltoid, mesially growing palatine plates followed by large

flat, posteriorly growing triangular plates above and a posteriorly growing symphysial plate; paired, small deltoid, laterally growing plates and a large, paired triangular and posteriorly growing set on the lower jaws. All small plates have large dentinal osteons forming tritoral lines, while the large plates have the typically tiny dentinal osteons of tubular dentine covering them completely. Among the many unique features of this fish are paired ethmoid claspers in the males which are derived from labial cartilages, squamation limited to the claspers and pelvic fins of males, a spineless, basidorsal-radial dorsal fin which runs the length of the back, dorsal and ventral hemicentra, and archipterygial pectoral fins.

A poorly understood Upper Devonian "cochliodont," *Synthetodus trisulcatus*, (Eastman, 1896; 1907) is named from a median and two elongate lateral plates on a base of calcified cartilage (fig. 1). While other plates are known, the reconstructed association here is entirely hypothetical. *Synthetodus* does evidence symphysial plates, however.

The second Bear Gulch fish is a chimaeroid, an acceptable member of Patterson's suborder Chimaeroidei, which differs from modern forms principally in lacking a mobile frontal clasper in the males and in having an extensive squamation. The implications of a Namurian chimaeroid upon phyletic considerations of the Holocephali are not small, and demand some reevaluation of the Mesozoic forms.

Dentition of the Chimaeroidei consists of small, anterior palatine tritoral plates followed by large, triangular posterior tritoral plates above and below (fig. 1). Squalorajidae differ from the modern Chimaeroidei chiefly in configuration of the plates and in adaptations concerning dorsoventral flattening, as well as in having a primitively extensive squamation (Patterson, 1965). The Chimaeropsidae differ in having palatine plates larger than the posterior uppers, and in having a lower symphysial plate. The large plates are covered in tubular dentine. Myriacanthidae differ in having two anterior small paired "palatine" tritoral plates, but otherwise resembling Chimaeropsidae.

For purposes of discussion a number of assumptions on evolutionary trends in bradyodont character complexes must be made. *Helodus*-like tooth families tend to fuse into transverse plates, as seen in *Helodus*, *Pleuroplax*, and menaspoids. Three tooth positions per jaw seems to be plesiomorphous, as seen in *Cochliodus* or

*Psephodus*, and the tendency in the group is to lose tooth positions, menaspoids and chimaeroids achieving two upper and one lower plate per ramus. Several members possess a mandibular symphy-sial dental element, probably also a plesiomorphous character as in *Synthetodus*, cf. *Platyxystrodus* and myriacanthoids; these fish are apomorphous in the reduction of anterior lateral elements.

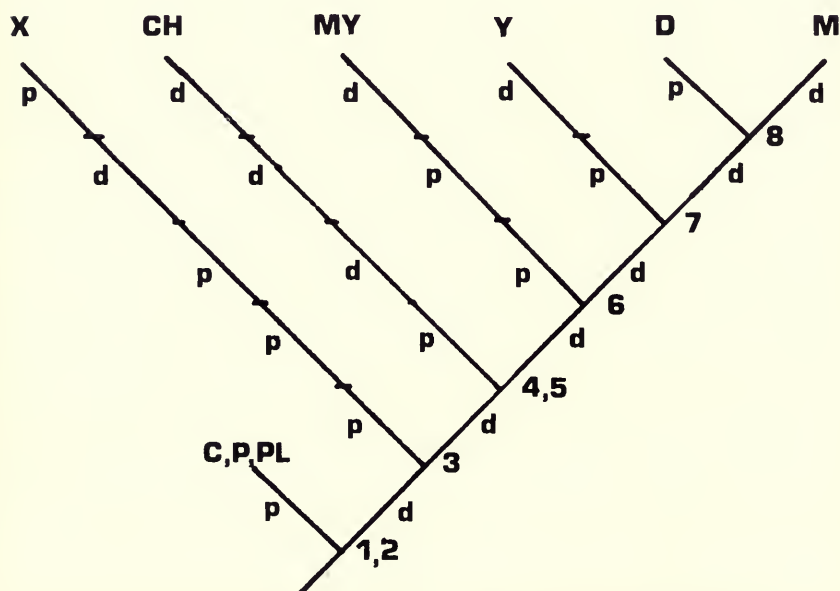
The enigmatic copodonts, known by symphy-sial elements, with occasional indications of minor lateral plates (Davis, 1883) may be related morphologically to *Synthetodus*. Psammodonts, known from lateral plates, may possibly be derivable from a dental arrangement of the type seen in *Psephodus minutus* (Moy-Thomas, 1934). Little definite can be said about these forms at present.

The presence of cranial plates and mandibular spines is common to the menaspoids, the *Physonemus*-like form and myriacanthoids, and is a defensive strategy presumably based on apomorphous fusion of dermal denticles. *Cochliodus contortus* lacks mandibular spines (Patterson, 1968). *Platyxystrodus* and the chimaeroids also share this plesiomorphous state, although both forms do display secondary sexual modifications of the squamation.

There are no known holocephalians with two dorsal fin spines. All forms which retain a dorsal fin spine of known morphologic relationship accompany it with a basal plate, radiating supporting elements and anteroposterior rotational mobility indicative of an articulation with the anterior portion of the vertebral column, a synarcual. The synarcual is not visible in either the Bear Gulch chimaeroid nor the *Physonemus*-like form and may not have been calcified, but can be inferred from the evident mobile dorsal spine and fin. Conversely, evolution of an antero-posteriorly mobile dorsal spine logically may be suggested as the reason for the origin of the synarcual in these fish, rather than primarily for cranial mobility. Forms like *Menaspis* and *Squaloraja*, secondarily flattened, retain a synarcual and can be inferred to retain it for pectoral stability or cranial mobility, as in rays; neither form retains a dorsal spine. *Platyxystrodus* has a plesiomorphously segmented anterior vertebral column and an elongate basidorsal-radial supported fin lacking a spine. This genus is autapomorphous in having an archipterygial pectoral fin, a structural arrangement quite subject to convergence (Lund, 1974).

*Helodus* is plesiomorphous relative to the Holocephali in chondrocranium, squamation, the presence of a heterocercal tail, and the dentition. It should be noted that *Helodus* dental development does

|   | C | P | PL | X | CH | Y | MY | D | M |
|---|---|---|----|---|----|---|----|---|---|
| 8 |   |   |    |   |    |   |    |   |   |
| 7 |   |   |    |   |    |   |    |   |   |
| 6 |   |   |    |   |    |   |    |   |   |
| 5 |   |   |    |   |    |   |    |   |   |
| 4 |   |   |    |   |    |   |    |   |   |
| 3 |   |   |    |   |    |   |    |   |   |
| 2 |   |   |    |   |    |   |    |   |   |
| 1 |   |   |    |   |    |   |    |   |   |



share with some edestoids and the more plesiomorphous holocephalian dentitions the tendency to fuse individual tooth replacement laminae into continuously growing tooth plates, a synapomorphous character. Other synapomorphous characters include the pectoral fin skeleton, holostyly, and form of the dorsal fins. *Helodus*, while not strictly includible within the Holocephali, is thus closely related to the taxon.

Cladistic relationships between known Holocephali are summarized in Figure 2. The psammodonts are omitted; if they are indeed derivable from a *Psephodus*-like morphology the plesiomorphous dental plate number may have been quite high (St. John and Worthen, 1883), close to the number seen in *Helodus*. Another systematic summary would simply burden the literature at this level of knowledge. It seems evident, however, that the myriacanthoids are not particularly close to the chimaeroids.

*Platyxystrodus* may possibly prove to be related to *Chondrenchelys* once the dentition of the latter is understood.

## PARASELACHII

Among the chondrichthyans to be considered in this category are the Iniopterygii, Helodontiformes, Edestiformes, and Petalodontiformes, as well as their relationships to each other and to the Holocephali. The common possession of a selachian dental plan and an operculum enfold a great variety of morphotypes.

INIOPTERYGII: The Iniopterygii have a symphysial tooth family and between five and eight lateral tooth families consisting of

### Opposite:

FIG. 2. Comparison of holocephalian character states, primitive, shaded blocks; derived, stippled.

| Primitive                 | Derived              |
|---------------------------|----------------------|
| 1. 3 paired lowers        | 2 paired lowers      |
| 2. 2 upper tooth families | 1 upper tooth family |
| 3. 2 paired lowers        | 1 paired lower       |
| 4. no cranial plates      | cranial plate        |
| 5. no mandibular spines   | mandibular spines    |
| 6. symphysial element     | loss                 |
| 7. 3 upper positions      | 2 upper positions    |
| 8. 1 upper family         | no upper families    |

C, *Cochliodus*; CH, *Chimaerid*; D, *Deltoptychius*; M, *Menaspis*; MY, *Myriacanthoid*; P, *Psephodus*; Pl, *Pleuroplax*; X, cf. *Platyxystrodus*; Y, physonemoid.

unicuspid to tricuspid teeth whose bases are fused into whorls (Zangerl and Case, 1973). Additionally, mucous membrane denticles fuse to form radiating patches in the roof of the mouth and on basal hyoid and branchial elements. Pennsylvanian forms from the mid-continental United States are strongly compressed, with dorsally placed, enlarged pectoral fins, a reduced posterior dorsal fin, and a small homocercal tail. The best-preserved Bear Gulch iniopterygian is depressed and broad skulled, the pectoral fin is large, chimaeroid-like anteriorly with a reduced axis and a trailing whip (fig. 3), the dorsal fin is very reduced, and the tail is modified heterocercal. Squamation is variably restricted to specialized, enlarged denticles on the snout, rim of the mouth, tips of the mandibles, and pectoral fins. Opercular rays are broad and well calcified in the Pennsylvanian forms. They are holostylic, although Zangerl (1974, pers. comm.) reports a free palatoquadrate in an unpublished form.

The simple marginal dentition of the iniopterygians in a moderate number of tooth families could easily serve as a plesiomorphous state from which a helodont dentition might be derived. The pectoral fin structure of the Bear Gulch form can also be considered plesiomorphous compared to the *Helodus* or chimaeroid condition. The Iniopterygii are autapomorphous in most other aspects of morphology.

**EDESTIFORMES:** This group has been classified as hybodont (Woodward, 1891; Radinsky, 1961), holocephalian (Obruchev, 1967), or split between the two groups on the basis of tooth histology and limited morphology (Bendix-Almgreen, 1968). The diversity of forms includes the orodontids *Orodus*, *Lophodus*, *Desmiodus*, *Agassizodus*, and *Campodus* from the Mississippian, *Ornithoprion* (Zangerl, 1966) and edestids from the Pennsylvanian and Permian, and Permo-Triassic Helicoprionids. Two holomorphs, one of which presently lacks a head, are known from the Bear Gulch.

The tooth shapes of edestoids vary from the helodontiform *Campodus* and *Lophodus* through elongate *Orodus*-type teeth to extremely elongate *Agassizodus* types. Symphysial and lateral tooth families may be basally fused, and symphysial dentitions are markedly enlarged in edestids and helicoprionids. Dentitions are also divergent from other paraselachii in their tendency toward accumulation in many members of many tooth families. Lateral teeth of most members consist of tubular dentine covered by pallial dentine, while sectoral symphysials may lack tubular dentine. In form and histology, the teeth are close to both hybodonts and primi-

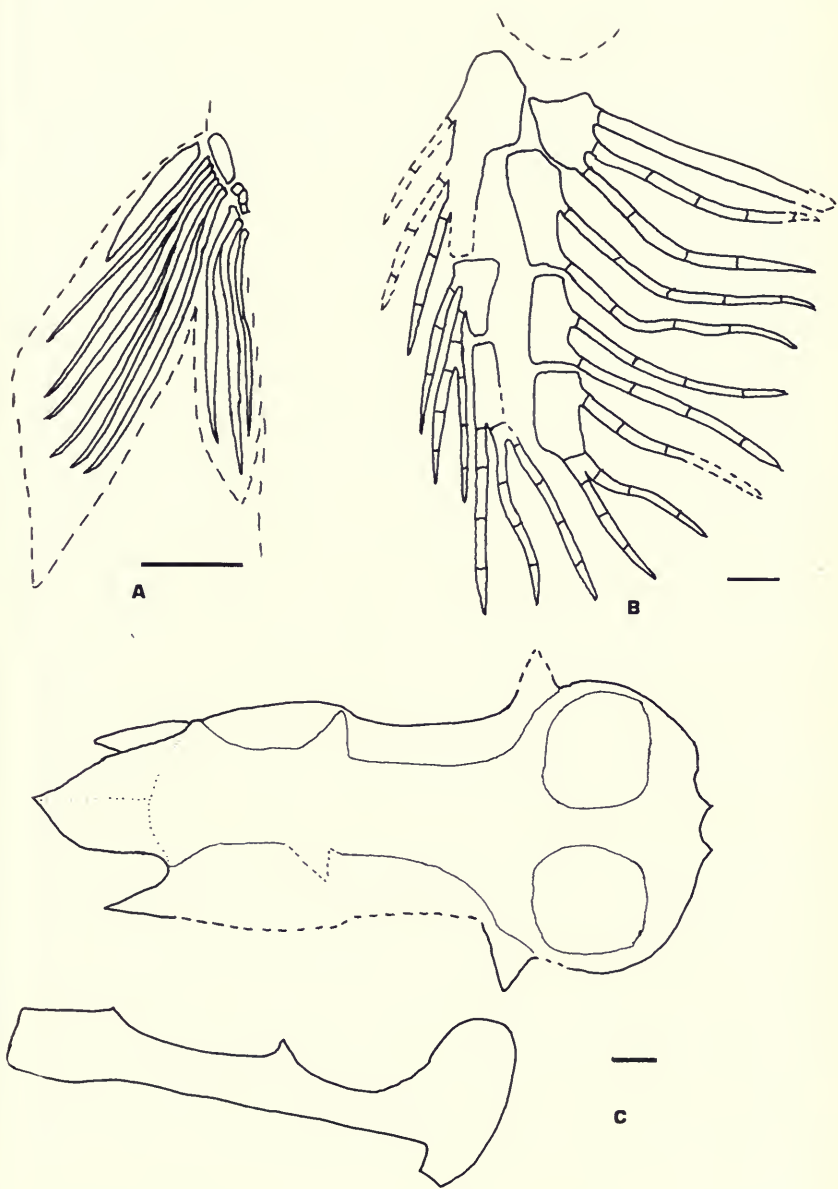


FIG. 3. Bear Gulch elements. A, Inioptergian, Carnegie Mus. 27425, left pectoral fin, skin outline dashed, Scale is 1 cm. B, Petalodont, Carnegie Mus. 23662, left pectoral fin. C, Petalodont, Montana vertebrate 2840, left individual, neurocranium in ventral view and palatoquadrate in lateral view, scale is 1 mm.

tive petalodonts (Agassiz *in* Davis, 1883; Woodward, 1891; Jaekel, 1899).

Palatoquadrates may be low, long, and free from the neurocranium or shortened and fused (Zangerl, 1966). A strong closed rostrum is present in some later forms (Bendix-Almgreen, 1968; Nielsen, 1952), but not in known earlier ones. The braincase, where known, is narrow and high orbitotemporally, quite short in the oticooccipital region and tapers rapidly to the foramen magnum. The postorbital process continues ventrally as a ridge. The known pectoral fins differ from a cladodont design in the great number of individual basal elements (Moy-Thomas and Miles, 1971). Squamation is complex (Zangerl, 1968). Two dorsal spines, the second followed by a ray-supported fin, are known in Bear Gulch forms. Caudal fins have neural and haemal arches and range from strongly heterocercal in one Bear Gulch form to almost diphyrcal and radial-supported in the other, where a large epichordal contribution is seen. Squamation of the former closely resembles that of *Orodus* (Zangerl, 1968). In later forms fusion of caudal arcuals produces a homocercal plate (Bendix-Almgreen, 1968). The Bear Gulch form has an operculum of long, thin, widely spaced rays.

Edestoid postcranial characters, such as the presence of two dorsal fin spines, the second supported by radials, the almost cladodont pectoral fin, and the heterocercal caudal fin with an epichordal contribution are strikingly different than other paraselachii. Pectoral and caudal structures can, however, be considered plesiomorphous for the bradyodonti. The squamation is unique, complex, and probably autapomorphous. Cranial characters of the later forms are autapomorphous, the craniums of earlier forms share more derived characters with Bradyodonti than with Elasmobranchii. Dentitional characters of form and histology are plesiomorphous with respect to helodonts, but are shared with early hybodonts as well (*Protacrodus* appears to share the same unique squamation, see Zangerl, (1968).) Tendencies toward fusion of the palatoquadrate and neurocranium are shared with bradyodonts; whether this character is plesiomorphous or apomorphous cannot now be determined.

The morphology of the edestoids is unique in its combination of elasmobranchian and bradyodont characters. An understanding of the earlier forms is critical to the early chondrichthyan radiation.

**PETALODONTIFORMES:** The petalodonts are known chiefly by their isolated teeth and dentitions, which are characterized by having cutting edges in vertically alternating shearing occlusion, lingual ridges, and roots which vary from short to quite long. The large variety of tooth shapes and dentitions fall into six groups, the *Ctenoptychius* group, the *Chomatodus* group, the *Climaxodus* group, the *Petalodus* group, the *Pristodus* group, and *Janassa*.

The *Ctenoptychius* group has a relatively homodont dentition of teeth with peaked, cuspidated, and moderately compressed crowns, slight lingual heel and folds, if any, and a short root. The ctenoptychians are central to the petalodont radiation, and are described as "orodonts squeezed flat" by Agassiz (*in* Davis, 1883).

The *Chomatodus* group has a heterodont dentition of few tooth positions and a marked elongation of the posterior teeth. Crowns range from arcuate to high and cuspidate anteriorly, to low, long, and swollen posteriorly with a strong set of ridges surrounding the tooth. Roots are long anteriorly, short posteriorly, and usually divided.

*Climaxodus* has a homodont dentition with relatively low swollen crowns, peaked at the symphysis and with a lingual heel and ridges and short roots. There is a symphysial tooth family, the remainder of the teeth are imbricated along the jaw margins.

The *Petalodus* group has a homodont dentition with compressed crowns peaked anteriorly, a pronounced heel and ridges, and long roots.

The teeth of *Janassa* can be derived from a *Petalodus*-like form by extreme emphasis on the development of the lingual heel. Teeth are arranged in a symphysial and three lateral rows in each jaw (Jaekel, 1899), producing a beak.

The *Pristodus* group has a homodont dentition of sharply compressed crowns, a lingual heel but no ridges, and short roots. The teeth are found in single series along the jaw margins and acrodonty may occur (Davis, 1883; St. John and Worthen, 1875; David, 1944; Obruchev, 1967; Lund, *in press*.)

A Bear Gulch petalodont near the *Ctenoptychius* group has long, thin, subdivided roots, slightly denticulated crests anteriorly, low, rounded crests posteriorly, and a sharp peaked symphysial tooth. There are four upper and five lower tooth families. It is round bodied, with a free palatoquadrate and small complex pectorals with

two articulated parallel rows of basals fringed with articulated bifurcating radials (fig. 3). This unique pectoral fin is found in another Bear Gulch petalodont. There is a single long dorsal fin led by a plain short spine lacking a basal plate. The pelvics are not joined in the midline, the tail is diphycercal, and the skin is naked. The neurocranium (fig. 3) is long preorbitally, with a precerebral opening, narrow orbitally, and has a short oticooccipital portion with a long dorsal groove. The strong postorbital process is not continued ventrally anterior to the swollen otic bullae. The palatoquadrate is long and free, and suspension is hyostylic (Lund, in press). An operculum is present. The Petalodontiformes share palatoquadrate, opercular, and dentitional characters with edestoids, but are unique in their dental radiation and the form of the pectoral fin. Among known chondrichthyans only *Tristychius* (Woodward, 1924) bears a pectoral fin resembling that of the petalodonts.

### SUMMARY

The Holocephali share a dental plate dentition which is apparently plesiomorphously limited to three lateral positions in each jaw plus a mandibular symphyseal element. Individual dental plates are derived phyletically from the fusion of members of a tooth family, the teeth being helodontiform in those taxa which retain them. Holostyly is plesiomorphous for the group. There is commonly a dibasal pectoral fin and two dorsal fins, only the first of which bears a spine; the caudal fin is diphycercal.

*Helodus* approaches the Holocephali in several shared derived dental characters, the form of the individual teeth, the tendency to fuse tooth families into transverse plates, and the form of these *Pleuroplax* plates. The structure of the pectoral fin, form of the dorsal fins, and holostyly are also characters shared with the Holocephali. Plesiomorphous characters include the low neurocranium, open precerebral fontanelle, the relatively high number of tooth families, and a heterocercal tail.

Primitive Iniopterygii share the structure of the anterior part of the pectoral fin skeleton with *Helodus*, and a short axis with edestoids and cladodont sharks; lengthening of the axial radials is an autapomorphous character. Simplicity of the marginal dentition is divergent from known chondrichthyans, but the number of tooth families approximates that of *Helodus*. Holostyly is also present, as is a plesiomorphous heterocercal tail.

Edestoid tooth morphology varies from a near-*Helodus* form through hybodont-like teeth to greatly elongate teeth. Later edestoids tend to have large numbers of teeth in many families, accompanied by enlarged symphysial teeth, holostyly, and strong closed rostrums. Like elasmobranchs, two dorsal fin spines may be present and the pectoral fin is cladodont-like but basally finely segmented. A heterocercal tail with an epichordal lobe, and a unique squamation may also be present. The palatoquadrate, where free, is long and low (Zangerl, 1966).

Primitive petalodonts seem to share a common tooth form with some edestoids, as well as a long, low palatoquadrate. Their neurocrania share characteristics with both elasmobranchs and holocephalians. In known fin structure and dental occlusion they are unique.

Among the paraselachii *Helodus* and the Iniopterygii share several derived characters, and a series of changes of character state between plesiomorphous conditions in edestoids and apomorphous in *Helodus* may be discerned. *Helodus* represents a plesiomorphous state of several critical characters relating to the Holocephali. Petalodonts show autopomorphous states of most character complexes, share a common (derived?) tooth form primitively, and display neurocranial characters which may, in the main, be plesiomorphous.

The edestoids share characters with other paraselachii and with elasmobranchs, but the evolutionary level of these characters seems to be primitive in respect to either one group or the other.

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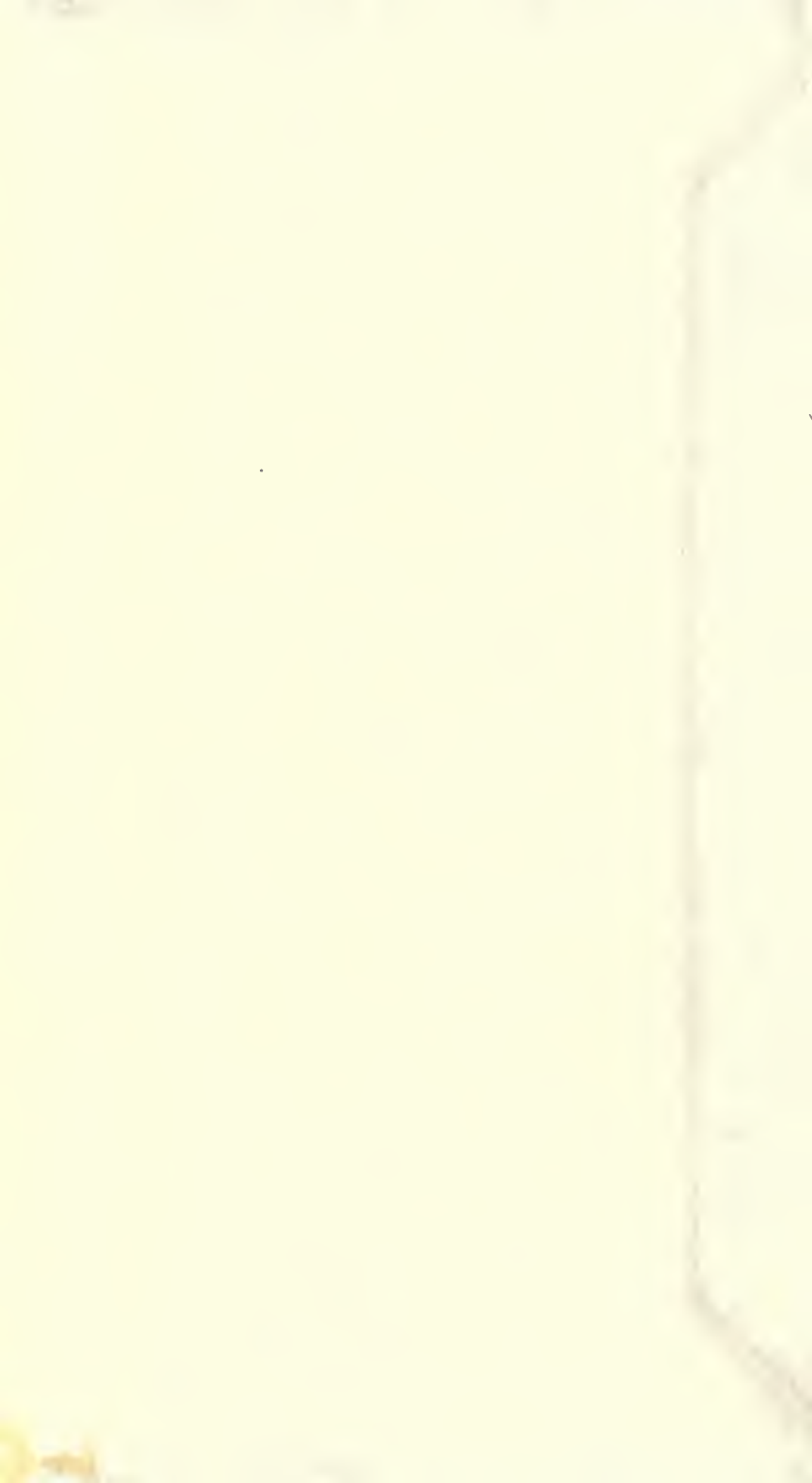












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